Article

A new genus and species of Western Atlantic sea lily in the family Septocrinidae (Echinodermata: Crinoidea: Bourgueticrinida)

ALEXANDR N. MIRONOV[1] & DAVID L. PAWSON[2]

[1]*P. P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Nakhimovskyi Prospekt 36, Moscow 117997, Russia.*
E-mail: miron@ocean.ru
[2]*D.L. Pawson, National Museum of Natural History, Smithsonian Institution, Washington DC 20013-7012, USA.*
E-mail: pawsond@si.edu

Abstract

Rouxicrinus vestitus new genus, new species, collected during submersible dives at depths of 421–887 m near Barbados, Colombia and the Bahamas is described, and notes on ecology are included. It is referred to the family Septocrinidae Mironov, 2000, which now comprises three genera, *Zeuctocrinus* A.M. Clark, 1973, *Septocrinus* Mironov, 2000, and *Rouxicrinus* new genus. This new genus differs significantly from both *Septocrinus* and *Zeuctocrinus* in having numerous low columnals in the proxistele, which tapers toward the crown, first pinnule arising more proximally, thorns on brachials and pinnulars, and a thick covering of soft tissue on arms and pinnules.

Key words: *Rouxicrinus vestitus*, Caribbean Sea, taxonomy, Crinoidea, Bourgueticrinida, Septocrinidae

Introduction

The family Septocrinidae is a small group of extant ten-armed sea lilies. The first-captured species of this group, *Zeuctocrinus gisleni* A.M. Clark, 1973, has been described in detail by A.M. Clark (1973), Roux (1977) and Roux *et al.* (2002). A.M. Clark (1973) referred *Zeuctocrinus* to the family Phrynocrinidae A.H. Clark 1907 comprising the extant *Phrynocrinus nudus* A.H. Clark 1907. This classification was followed by Rasmussen (1978), but Bourseau *et al.* (1991) and Roux *et al.* (2002) assigned *Zeuctocrinus* to Bathycrinidae Bather, 1899. Mironov (2000) established the family Septocrinidae for *Septocrinus disjunctus* Mironov, 2000, *Zeuctocrinus gisleni* and *Z. spiculifer* Mironov, 2000. Further support for establishment of the Septocrinidae was provided by Mironov (2008). Representatives of this family have not yet been subjected to molecular analysis.

Septocrinids were known previously only from five captures. *Z. gisleni* was recorded west of Northern Ireland and from the Bay of Biscay, depths 2000–2432 m (A.M. Clark, 1973; Roux, 1977). *S. disjunctus* has been collected from the Argentine Basin, depth 5180–5190 m; *Z. spiculifer* is known from the southern Izu-Bonin (Izu-Ogasawara) Trench, 6780–6785 m (Mironov, 2000). Breimer (1978, Figure 13.4) figured an undescribed species as a presumed *Zeuctocrinus* from the Antarctic.

Until now, *Bathycrinus caribbeus* A.H. Clark 1908a was the only species of ten-armed sea lily known from the western tropical Atlantic. This species was established on the basis of incomplete specimens with basal ring and column; the radial ring and arms were lacking. *B. caribbeus* was transferred to the genus *Monachocrinus* A.H. Clark by Gislén (1938). The type specimen was collected NW of Guadeloupe at a depth 1257 m (*Albatross* station 2751). Subsequently, representatives of *M. caribbeus* were reported from other areas of the western Atlantic (H.L. Clark, 1941, Gislén, 1951; Meyer *et al.*, 1978), but they were not described.

Two other bathycrinid species were reported from the western areas of the Atlantic Ocean. *Bathycrinus serratus* was established on the basis of incomplete specimens, taken off the coast of Virginia and Maryland in depths of 3340–3680 m (A.H. Clark, 1908b). According to Gislen (1951), this species is synonymous with *B.*

aldrichianus Thomson. A.M. Clark (1977) recorded *B. aldrichianus* again from the east coast of the U.S.A (SE of New York), at a depth of 3834 m, and also from the northern coast of Argentina (SE of Rio de la Plata), in 3305–3317 m. *B. australis* A.H. Clark is another bathycrinid species collected from off Rio de la Plata, in 2707–5223 m (A.M. Clark, 1977). In addition, an undescribed bathycrinid species was taken by R/V *Columbus Iselin* in the Bahamas area, at depths of 4243–4558 m (unpublished data). This last species is believed to belong to the genus *Discolocrinus* Mironov, 2008.

This paper describes a new genus and species *Rouxicrinus vestitus* in the family Septocrinidae. Specimens were collected near Barbados and the Bahamas during dives of the *Johnson-Sea-Link* submersibles (Harbor Branch Oceanographic Institution, Inc.) in 1988-9. New data confirm the taxonomic significance of pinnule structure in the Bourgueticrinida. Data provided by the new genus also necessitate modification of the diagnosis of the family Septocrinidae.

Terminology: Character terminology of calyx, arms and stalk follows that of Breimer (1978) and Roux *et al.* (2002). The following traditional abbreviations and symbols are used: BB—basals, RR—radials, Br—brachial, Brax—axillary, IBrs—primibrachials (first brachitaxis following a radial), IIBrs or Brs—secundibrachials (second brachitaxis following the first axillary), the Roman number following Br indicates the rank into a given brachitaxis (for example, Br3 is the third secundibrachial), a sign (+) indicates a non-muscular (ligamentary) articulation uniting a brachial pair (for example Br3+4), P—pinnule, P1—first pinnule, Pn—pinnular, Pn1—first pinnular. The arm pattern is usually simplified by indication of brachial pairs only (for example, Br1+2 3+4 8+9 13+14 … consequently, brachial pairs 3+4 and 8+9 are separated by four successive muscular articulations). The dimensional parameters measured on calyx, primibrachials and columnals are detailed in Mironov, 2000, fig. 1.

Order Bourgueticrinida Sieverts-Doreck 1953

Family Septocrinidae Mironov, 2000

Diagnosis. Aboral cup inverted conical, much broader than high. All sutures between basals and radials conspicuous. Basal and radial circlets almost equal in height or radials higher than basals. Tegmen not inflated, with prominent anal sac. IBr1+2 ax, primibrachials without inner knobby processes. Maximum number of consecutive muscular articulations in free arms from 6 to16; brachial pair IIBr1+2 united by transverse synarthry (not known for *Zeuctocrinus*); beyond IIBr2, flat and smooth synostoses, the first at IIBr3+4, the second usually from 7+8 to 9+10 (7+8 to 13+14 in *Rouxicrinus*), the others irregularly placed. First pinnule on Br6 to Br12. Pinnules without cover plates, lateral plates and x-like spicules on tube-feet; ambulacral grooves with two rows of curved rod-like spicules and sacculi; pinnulars crescentic in cross-section (not V-shaped). Proximal pinnules free, not attached to tegmen. Discoid proximal columnals single to numerous, proximalmost columnals one-pieced or compound. Distal synathries circular to ovoid with irregular relief on fulcral ridge. Distal stalk attachment by root-like radix

Included genera : *Septocrinus* Mironov, 2000, *Zeuctocrinus* A.M. Clark, 1973, *Rouxicrinus* gen. nov.

Remarks: The following features have been used as the main diagnostic characters for *Septocrinus* (the main differences from *Zeuctocrinus gisleni* and *Z. spiculifer*): (1) high distal interradial projections of radials, (2) long median prolongation in IBr2 and (3) compound structure of most proximal columnals (Mironov, 2000).

Extant ten-armed Bourgueticrinida exhibit six types of pinnule structure (Mironov, 2008), one of which is unique to the Septocrinidae. However, pinnule form and structure in Septocrinidae is closely similar to that of some comatulids, for example *Antedon tenella*, *A. bifida*, (Grieg, 1903, figs. 3A, 3C), *Trichometra cubensis*, *Hypalometra defecta*, *Hathrometra prolixa* (A.H. Clark, 1921, figs. 766, 768, 775), *Phrixometra nutrix*, *Isometra vivipara*, *I. flavescens* (John, 1938, figs.11, 15, 16). These comatulid species and septocrinids all have pinnulars crescentic in cross section, with rod-like spicules, and sacculi in the ambulacral grooves. Cover (ambulacral) and x-like tube feet plates are common in living Bathycrinidae (cover plates are lacking only in *Discolocrinus* Mironov, 2008) are absent in septocrinids.

Distolateral corners of adjacent RR in *Septocrinus disjunctus* form narrow triangular interradial projections separating bases of adjacent rays (Mironov, 2000, fig. 7.*4*). The long interradial projections of the radials are known also in many comatulids and some extinct cyrtocrinids (Phyllocrinidae Jaekel, Eugeniacrinitidae Roemer, Nerocrinidae Manni and Nicosia). The interradial ridges have wide intraspecific variation in the Eocene genus *Tormocrinus* Jaekel, and they are weakly developed in fossil *Conocrinus* Orbigny (Bourgueticrinidae) (Roux, 1978). Another unusual feature in *Septocrinus* is a large median prolongation of IBr2ax, located between the two following elements. Similar prolongation of IBr2ax is known also in some extinct cyrtocrinids (*Eugeniacrinites* Miller, *Lonchocrinus* Jaekel). The compound proximal columnals is a stable feature of *Septocrinus disjunctus,* being well developed in all three known specimens. Fragmentation of the proximal columnals is otherwise unknown in the Bourgueticrinida, but is particularly well developed in *Vityazicrinus petrachenkoi* Mironov and Sorokina (Vityazicrinidae), *Dumetocrinus antarcticus* (Bather) and *Feracrinus aculeatus* Mironov and Sorokina (Hyocrinidae). The proxisteles of *Septocrinus, Vityazicrinus, Dumetocrinus* and *Feracrinus* with compound proximal columnals probably resulted from long evolutionary changes (See below "Notes on ecology and morphological adaptations").

Septocrinidae also differ from the Bathycrinidae (sensu stricto) in the following characters: (1) no inner knobby processes on IBr ossicles (SEM micrographs of these processes in *Bathycrininus aldrichianus* can be found in Macurda and Meyer, 1976, Pl. 3. *5* and in *B. mendeleevi* by Mironov, 2008, Figure 4C), (2) another proximal free arm pattern: from 1+2 3+4 7 to 1+2 3+4 9 (usually 1+2 3+4 5 or 1+2 4+5 7 in *Bathycrinidae*), (3) great number of consecutive muscular articulations in the distal arm, (4) almost flat and smooth synostoses beyond IIBr2 (rudimentary transverse synarthry in *Bathycrinus*), (5) few discoidal columnals in *Septocrinus* and largest *Zeuctocrinus* (but about 10 in the smallest paratype of *Z. gisleni* and more than 30 discoid columnals in *Rouxicrinus*) (usually 10 columnals or more in Bathycrinidae), (6) irregular syzygial stereom on the fulcral ridge of the distal columnals (regular secondary crenularium in the Bathycrinidae except for *Bathycrinus volubilis* Mironov, *Discolocrinus thieli* Mironov), (7) dense arrangement of Ps: when viewed from the side, every second or third Br bearing a P (P on every fourth Br in Bathycrinidae).

Septocrinidae differ from the ten-armed *Caledonicrinus* Avocat and Roux and *Naumachocrinus* A.H. Clark in having developed BB and radix, more distal position of P1, and in lacking cover and side plates (pinnule structure not known for *Naumachocrinus*).

Among the crinoids with five unbranched arms (*Democrinus* Perrier*, Conocrinus* Orbigny*, Porphyrocrinus* Gislén) and with arms branched beyond IBr2 (*Phrynocrinus* A.H. Clark*, Porphyrocrinus thalassae* Roux) , *Phrynocrinus* shares several features with *Septocrinus* and *Zeuctocrinus*. All three genera have rod-like spicules in the ambulacral grooves, an oblique fulcral ridge on the muscular brachial articulations, almost smooth non-muscular brachial articulations (synostoses), and proxistele absent or with a few discoidal columnals. However *Phrynocrinus* differs significantly from septocrinids also in possessing a lobed stalk attachment disk, strongly inflated tegmen, and very long proximal pinnules attached by thick bases to the tegmen (A.H Clark, 1907; A.M. Clark, 1973; Imaoka *et al.*, 1991, Donovan & Pawson, 1994; Kogo, 1998; Roux *et al.*, 2002).

Rouxicrinus **new genus**

Etymology: The genus is named for Michel Roux, Muséum national d'Histoire naturelle, Paris, France, in recognition of his contributions to our knowledge of the crinoids.

Diagnosis: Proxistele tapers towards the calyx. Discoid columnals in proxistele numerous, usually more than 30, and united by flat synostoses. Columnals of mesistele short; maximum ratio height/diameter of columnals 1.68. Articular facets of mesistele synarthries ovoid, with wide fulcral ridge along smaller diameter; those of distal synarthries circular. First primibrachials (IBr) separated by well developed interradial projections of radials in small specimens only. Median distal prolongation of IBr2 absent. IBr1 shorter than radials . Maximum number of successive muscular articulations in arms 6–10. Most frequent proximal free arm pattern1+2 3+4 9+10 or 10+11; first pinnule on IIBr6–8 (mode on IIBr7). When viewed from the side,

every second or third Br bearing a P. Stereom of secundibrachials and pinnules with coarse meshes and many needle-like projections giving external surface dissected and thorny especially in distal ossicles. Thorns along upper margin of brachials and pinnulars. Second pinnular shorter than first; third pinnular longer than first in proximal pinnules.

Type species by monotypy: *Rouxicrinus vestitus* new species.

Remarks: This new genus differs significantly from both *Septocrinus* and *Zeuctocrinus* in having numerous low columnals in the proxistele, tapering proximal end of stalk, a more proximal position of P1, thorns on the Brs and Pns, and a thick cover of soft tissue. The distolateral interradial projections of RR in smaller specimens are a feature shared with *Septocrinus*, but not found in *Zeuctocrinus*. In life, all specimens of *Rouxicrinus* have a white stalk, light cream calyx and Brs, Ps reddish purple; in alcohol stalk white, Ps brownish-violet. *Septocrinis* and *Zeuctocrinus* are monochromatic, light yellowish grey to whitish in alcohol. This colour corresponds to bright yellow in life (like in most hyocrinids); confirmed for *Z. gisleni* observed from submersible in Bay of Biscay and on Porcupine bank (M. Roux, pers. com.). Table 1summarizes these and other differences.

According to Meyer at al. (1978), representatives of two other bourgueticrinid genera, *Democrinus* Perrier and *Monachocrinus* A.H. Clark, are known from the western Atlantic, from south Florida to Rio de Janeiro, Brazil (including the Caribbean Sea, Gulf of Mexico and Bahama Islands). *Democrinus*, with 5 arms, can be immediately distinguished from *Rouxicrinus vestitus*. The available information on *M. caribbeus* is not sufficient to enable a detailed assessment of its generic or family position, although the holotypes of *B. caribbeus* and *R. vestitus* are clearly not conspecific. The holotype of *M. caribbeus* is well distinguished from *R. vestitus* by its high basal ring (taller than broad), fused BB, few discoid proximal columnals (the 10th columnal is higher than broad), and ovoid distal stalk articular facets (A.H. Clark, 1908a, 1908b, 1915; Gislén, 1938, 1951).

Rouxicrinus vestitus new species
Figures 1–10

Etymology: The species name is derived from Latin *vestis*, a garment, in reference to the covering of soft tissue on the secundibrachials.

Diagnosis: As for the genus.

Material examined: Five specimens, collected using the submersible Johnson-Sea-Link (HBOI) on housed in the National Museum of Natural History, Smithsonian Institution, Washington DC, USA. Holotype: USNM catalogue number E00042699**,** specimen collected by D. Billett and G. Hendler during dive JSL-II-1737 off Speightstown, Barbados, 13°15'06"N – 59°45'04"W, depth 747 m, 20 April, 1989. Two paratypes: (1) USNM catalogue number E00042707, specimen collected by D. Pawson and D. Billett during dive JSL-II-1729 off Barbados, 13°15'30"N – 59°45'47"W, depth 876 m, 16 April 1989; (2) USNM catalogue number E00042700, specimen collected by C. Young and J. Miller during dive JSL-II-1731 off Barbados, 13°16'17"N – 59°45'24"W, 816 m, 17 April 1989. Other material: (1) USNM catalogue number 1021239, specimen collected by D. Pawson and D. Billett during dive JSL-I-2268 off Bahamas, Crooked Island Passage between Long Island and Crooked Island, 22°41'23"N–74°21'18"W, depth 887 meters, 15 September 1988; (2) USNM catalogue number E0017898, specimen collected during cruise 6607 of RV Pillsbury, St. 394-1 off Fuerte Island, Colombia, 9°28'36"N, 76°26'18"W, 421–641 m, 16 July 1966.

Description: In life, all specimens with stalk white, calyx and Brs with light cream tint, Ps reddish purple.

HOLOTYPE. (Figures 1, 2, 4A,B,D,F, 5, 6). Complete specimen except two arms broken at IBr3 with two short isolated fragments only, total length from base of radix to distal top of crown 155 mm. Calyx regularly conical without angle between basal and radial rings; interbasal and interradial sutures conspicuous. Distal margin of RR U-shaped; distolateral corners of adjacent RR forming narrow triangular interradial projections separating bases of adjacent rays (Figure 1). Interradial calyx height 1.9 mm (including length of interradial projections); maximum and minimum calyx diameter 2.5 and 1.1 mm; ratio of BB to RR height 0.61**;** surface of BB, RR and IBrs smooth without ornamentation.

TABLE 1. Differences between species of the family Septocrinidae.

Characters	Rouxicrinus vestitus	Septocrinus disjunctus	Zeuctocrinus gisleni	Zeuctocrinus spiculifer
Maximum calyx diameter (mm)	4.12– (2.5 in young)	3.5	5.2 (1.8 in young)	1.8 (? young holotype)
Distal interradial projections of radials	Well developed in small specimens	Well developed	Slightly developed or absent	Slightly developed or absent
Interrradial tegmen (height relative IIBr level)	Br4–5 (2–3 in young)	Br7–8	Br7*	IIBr1
Anal sac (top relative to IIBr level)	IIBr7 (3–4 in young)	Br10	Br12*	IIBr2
Median prolongation in IBr2	Absent	Present	Absent	Absent
Ratio IBr1/RR heights	< 1	> 1	> 1	< 1
Most frequent position of P1	Br 7	Br10	Br10	Br12
Most frequent proximal brachial formula	1+2 3+4 9+10 and 1+2 3+4 10+11	1+2 3+4 7+8	1+2 3+4 7+8	1+2 3+4 10+11
Maximum number of successive muscular articulations	9	7	9	16
Presence of P on the middle and distal Brs	Some Brs without P	Some Brs without P	Some Brs without P	All Brs with P
Thorns on Brs and Pns	Present	Absent	Absent	Absent
Ratio Pn2/Pn1 in proximal Ps	< 1	1 to < 1	?	> 1
Maximum ratio Pn3/Pn1	1.43	1.20	?	3.65
Tip of the stalk	Usually tapering (upwards)	Not tapering	Not tapering	Not tapering
Number of columnals in proxistele (ratio height/diameter <0.3)	~30	1–5	1–4 (up to 1 in young)	1
Structure of most proximal columnals	Monolithic or with indistinct longitudinal sutures	Clearly compound	Monolithic	Monolithic
Articulations in proximal stalk	Flat synostoses	Synarthries	Synarthries	Synarthries
Articular facets of distal columnals	Circular synarthry with deep areola	Ovate synarthry with deep areola	Subcircular flat synarthry	Unknown
Maximum ratio height/diameter of columnals	1.7	1.4	0.6 (up to 1.9 in young)	? (2.1 in columnal 10)
Covering of soft tissue on proxistele, calyx and Brs	Conspicuous	Inconspicuous	Inconspicuous	Inconspicuous
Colour (in alcohol)	Brownish-violet arms and white stalk	Monochromatic, light yellowish-grey to whitish	Monochromatic, light yellowish-grey to whitish	Monochromatic, light yellowish-grey to whitish

* M. Roux, pers. com.

Tegmen with an axis of bilateral compression running from interradius AB to radius D, arising radially to distal margin of Br3, interradially to distal margin of Br1 or base of Br2. Some tegminal (oral?) plates of irregular shape visible in peristomial elevation. Top of prominent anal sac level with middle of Br3, 1.4 mm high.

Length of primibrachitaxis (IBr1+2ax) 2.5–2.6 mm; ratio of IBr1 to IBr2 height ~0.7; that of IBr1/RR 0.8. IBrs broader distally than proximally, much broader than long with sides slightly flattened into lateral flanges not continuing in free arm bases; IBr2 without interradial projection between neighboring IIBrs1.
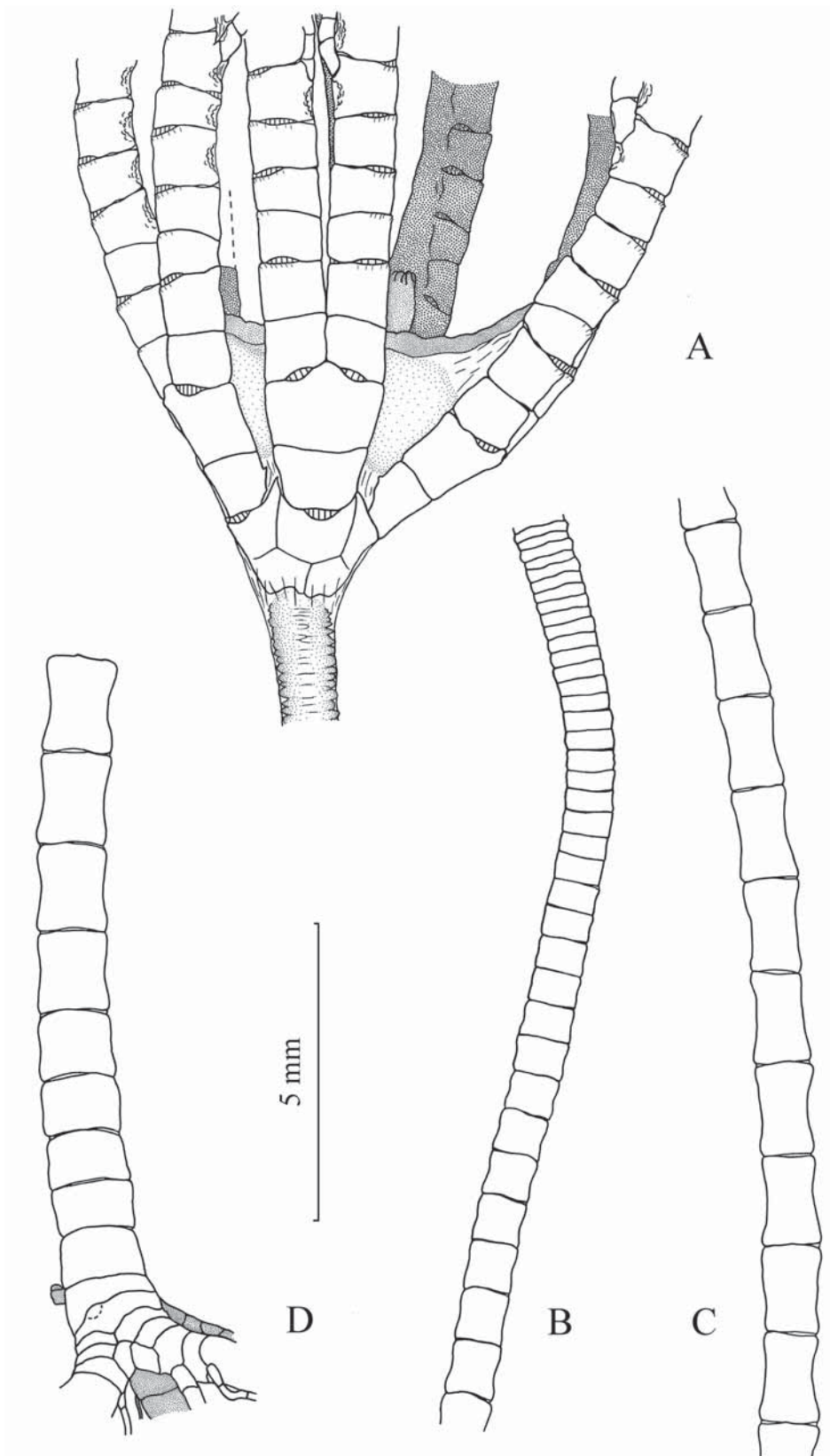
FIGURE 1. *Rouxicrinus vestitus* new genus, new species, Holotype, USNM E00042699. A. Calyx with proximal parts of stalk and arms. Prominent anal sac visible between diverging arms. B. Stalk (parts of proxistele and mesistele) between 16th and 51st columnals. C. Stalk (part of mesistele) between 77th and 86th columnals. D. Stalk (dististele) between 121st columnal and root-like radix.

Length of complete free arms up to 23 mm, ends of arms and pinnules usually rolled inward. Secundibrachials 45 to 54 in number. Proximal pattern with IIBr1+2 3+4, and 8+9 (5 cases), 6+7, 7+8, 9+10 (1 case each). Beyond the third, positions of non-muscular joints irregular in median and distal free arms (types of joint usually indistinguishable in distalmost part) illustrated by three following examples (1) 11+12 18+19 20+21 27+28 34+35 39+40, (2) 14+15 18+19 24+25 30+31, (3) 16+17 22+23 29+30. Never more than 6 successive muscular articulations observed. Muscular brachial articulations having classical features, inner ligament areas with galleried stereom, and slightly oblique fulcral ridge (Figure 4B). Transverse synarthry without symmorphy and with relatively wide fulcral ridge at IIBr1+2 (Figure 4C). Ligamentary articulation of more distal IIBrs flat and smooth synostosis, except short culmen at mid-adoral margin (Figure 4A).

IIBrs and Pns covered by transparent film of soft tissue; labyrinthic stereom with coarse meshes and many needle-like projections, producing a dissected and thorny surface, especially on distal Brs and Ps. Thorns lie along distal margin of Brs and Pns (Figures 2B, 4D, 5F).

On one side of an arm, maximum number of Ps 15, every second or third Br bearing a P. P1 on Br7 on four arms, Br6 on two arms, Br8 on two arms and lost on two arms (arms broken at Brs3). P1 of 13–14 Pns; maximum length 6.2 mm. P2–P4 of 15–16 Pns, up to 7.5 mm in length. Muscular synarthry between Pn1 and Pn2 (Figure 5D); with typical characters remaining visible up to Pn9.
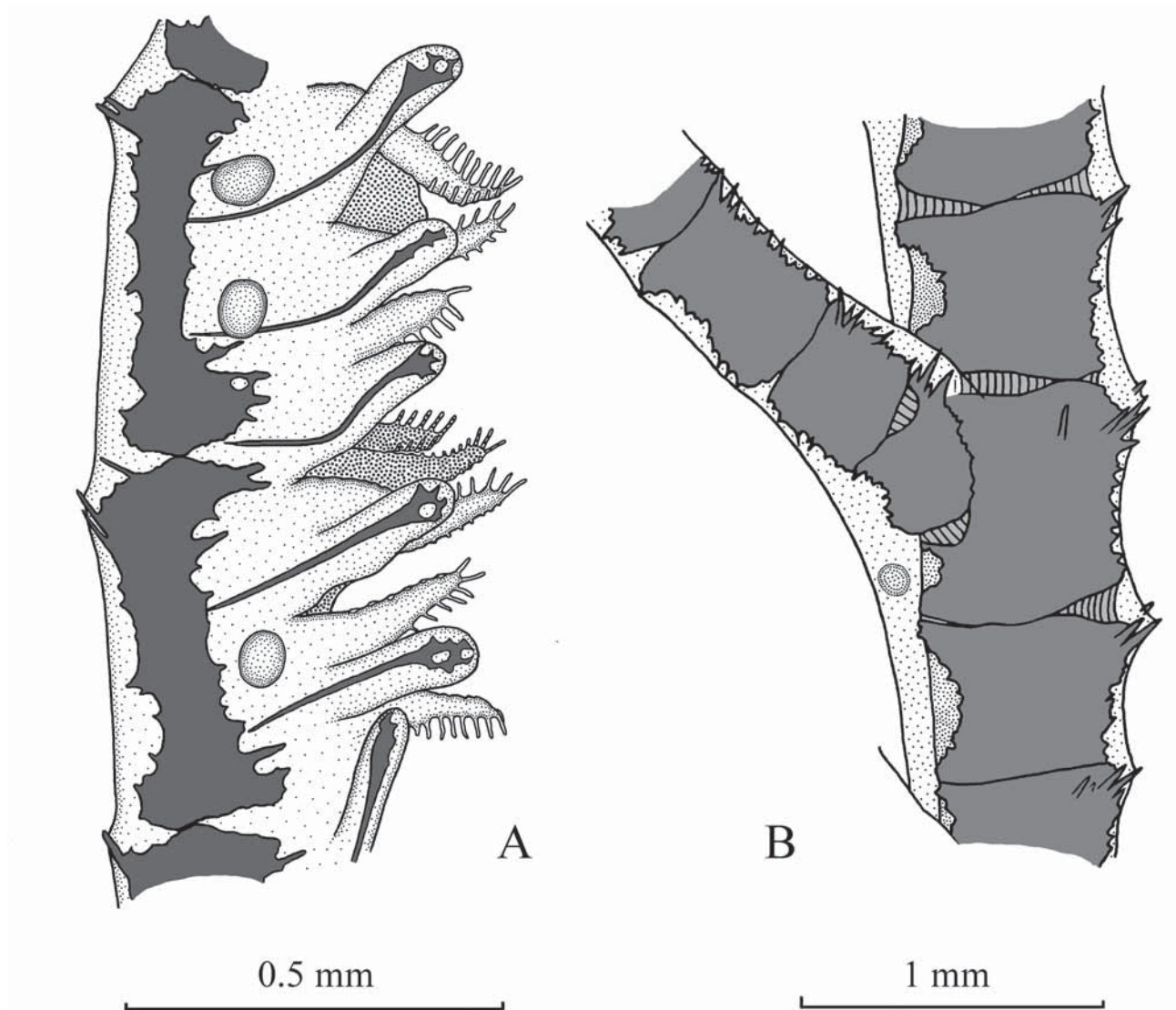

0.5 mm   1 mm

FIGURE 2. *Rouxicrinus vestitus* new genus, new species, Holotype, USNM E00042699. A. Scheme, showing position of rod-like spicules and sacculi in relation to pinnulars and tube feet; viewed from the side (showing base of pinnulars 10 and 11 of the pinnule 3 of the arm D8). B. Brachials 17, 18 and 19, and proximal part of pinnule 5.
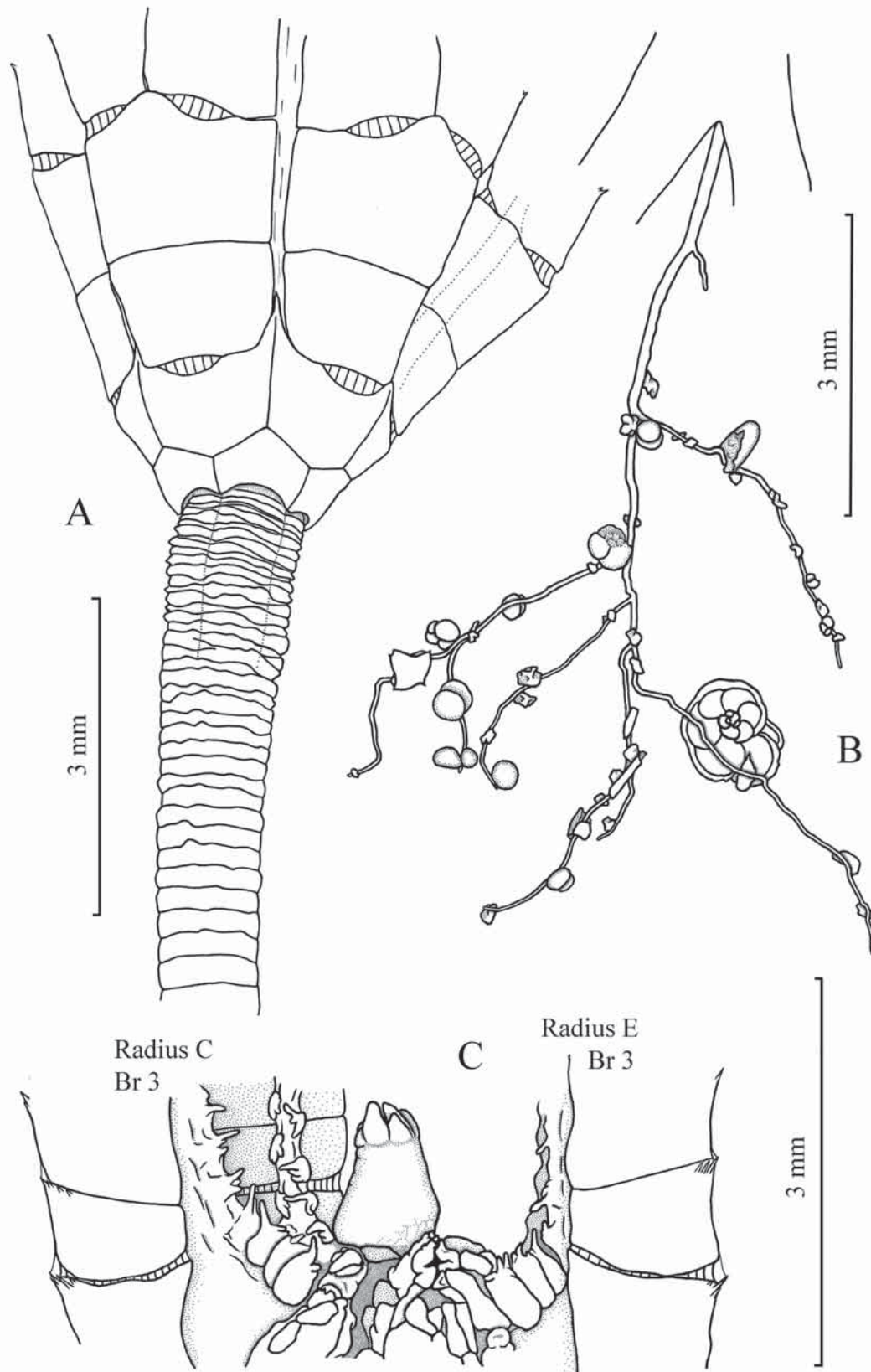
FIGURE 3. *Rouxicrinus vestitus* new genus, new species, Paratype, USNM E00042707. A. Calyx with proximal parts of stalk and arms. Distal interradial projections of calyx visible between primibrachs. Soft tissue removed. B. One of thin radicle branches attached to grains of sand and foraminiferal tests. C. Anal sac and adoral triads of ambulacral tube-feet; each triad with high columnar base with thin lacy plates.
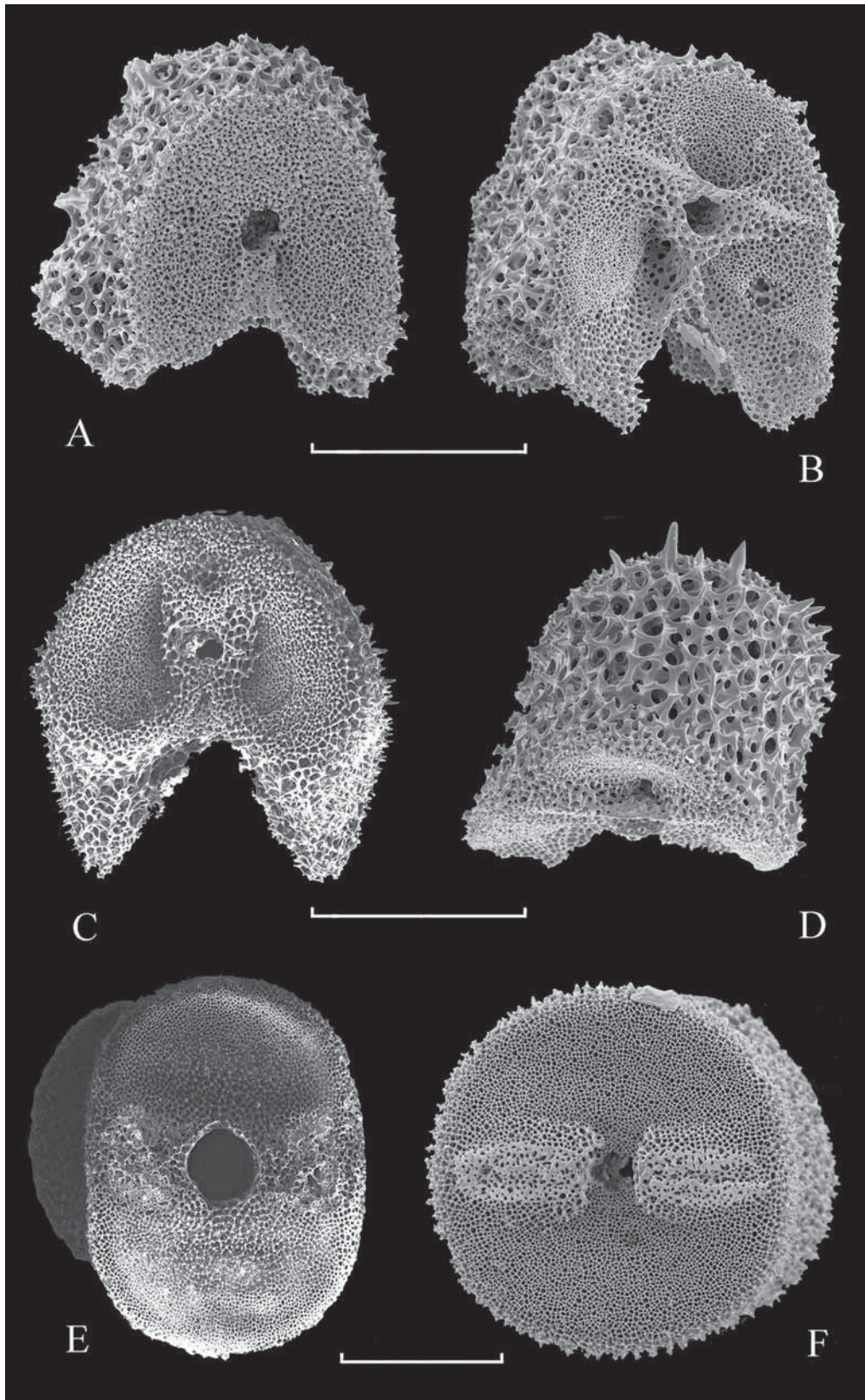
FIGURE 4. *Rouxicrinus vestitus* new genus, new species, Holotype, USNM E00042699 (A, B, D, F), and paratype, USNM E00042707 (C, E). A, Proximal articular facet of Br15, non-muscular joint (synostosis). B,Distal articular facet of Br13, muscular synarthry. C, Proximal articular facet of IIBr2, non-muscular joint with rudimentary dorsal concave areola (transverse synarthry). D, Br12, view from exterior. E, synarthrial facet of columnal 102 (mesistele) with fulcral ridge along the smaller diameter. F, articular facet of columnal 124 (dististele) with fulcral ridge along the longer diameter. Scale: 500 µm.
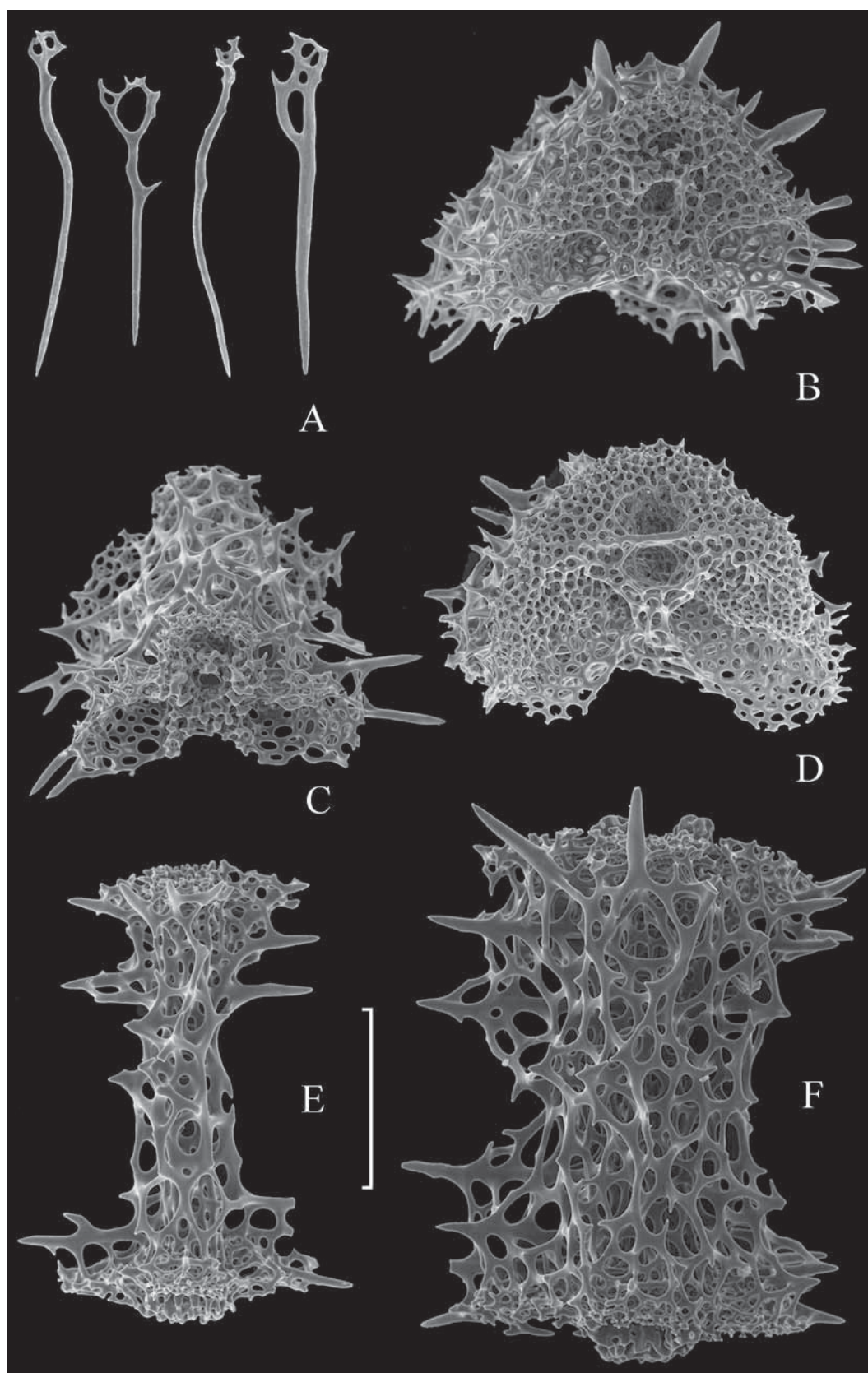
FIGURE 5. *Rouxicrinus vestitus* new genus, new species, Holotype, USNM E00042699. Ossicles of pinnule 3 of arm D8. A, Rod-like spicules which border ambulacral groove. B, Distal articular facet of Pn3. C, Distal articular facet of Pn8. D, Proximal articular facet of Pn2. E, Pn11, viewed from exterior. F, Pn7, viewed from exterior. Scale: 200 μm.

FIGURE 6. *Rouxicrinus vestitus* new species, Holotype, USNM E00042699. A, Crown with proximal portion of stalk. Total length of this fragment 39 mm.. B, Radix. Total length of this fragment 23 mm. Photos: John E. Miller, Harbor Branch Oceanographic Institute at Florida Atlantic University/Smithsonian Institution.

Relative length of Pns variable, Pn2 shorter than Pn1 (ratio 0.8–0.9) in proximal Ps; Pn3 always much longer than Pn1 (ratio more than 1.3); in P2 and P4 of a given arm, ratios relative to Pn1 length decreasing from 1.35–1.43 for Pn3 to 0.8 (P2) or 1.1 (P4) for Pn13. Pns crescentic in cross section, not V-shaped, with thorns along distal margin (Figure 5B–F). Each ambulacral groove bordered on both sides by rod-like spicules and spherical bodies of soft tissue (sacculi) (Figures 2A, 5A); spicules 0.30–0.45 mm long, curved, widening at distal end, pointed proximally (Figure 5A); some spicules (especially in base of proximal Ps) branching distally; each spicule covered by transparent soft tissue (lappet). Cover and side plates absent. Sacculi cream-coloured, embedded in soft tissue with diameter 0.07–0.09 mm. Lappets in brachial ambulacral grooves with rod-like spicules or thin lacy plates; sacculi more elongated than those in Ps. Genital pinnules not distinguishable morphologically.

Remaining proximal part of stalk (72 columnals) attached to aboral cup 44 mm long. Total stalk length from calyx to base of radix, ~128 mm, of 128–131 columnals, consisting of proxistele attached to calyx and two stalk fragments (Figures 1B–D).

Stalk diameter increases slightly from columnal 1 (1.0 mm) to 7 (1.1 mm), decreases to 0.8 mm between columnals 8 and 35 (Figure 1B), remains the same from 36 to 74 (~0.8–0.9 mm), and increases slowly

beginning at 75 to 1.4 mm by columnal 130 (Figures 1C and 1D). Height increases from 0.1 to 1.5 mm between columnal 1 and 72, remains unchanged (~1.4–1.6 mm) from 73 to 107, increases to 1.9 between 108 and 122, and decreases to 0.8 mm between 123 and 128. Height/diameter ratio increases from 0.16 for columnal 16 to 1.68 on 72, with columnal 48 as long as broad (Figure 1B), and decreases to 0.58 between 73 and 128 (Figure 1C).

Proximal columnals are monolithic or with indistinct longitudinal sutures. Median constrictions of columnals slightly or moderately developed in mesistele (Figure 1C), disappearing in four distalmost columnals (Figure 1D). Flat circular synostoses in proxistele, ovoid synarthries with coarse fulcral ridge along smallest diameter in mesistele (Figure 4E), circular synarthries with well developed fulcral ridge and large deep areola in dististele (Figure 4F). Distal synarthries with pentagonal lumen (0.12 mm of facet diameter) and fulcral ridge of irregular relief (Figure 4F). Root-like radix, well developed. Thick basal part of radix consists of numerous coalesced ossicles (Figure 1D); sutures almost invisible. Distal radicles long, very thin, attached to numerous grains of sand and foraminiferal tests (Figure 6B).
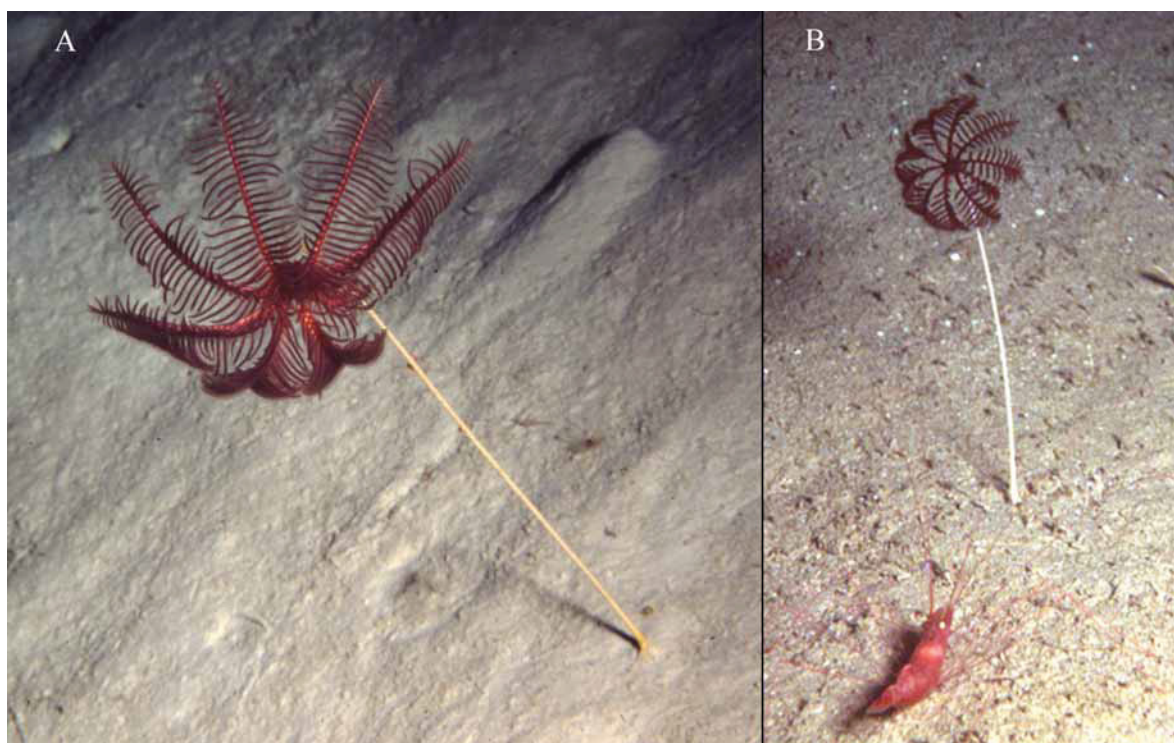

FIGURE 7. *Rouxicrinus vestitus* new species. Specimens *in situ*. A, Specimen USNM 1021239 from Dive JSL-I-2268. B, Paratype specimen USNM E00042700, Dive JSL-II-1731. Photos: Harbor Branch Oceanographic Institute at Florida Atlantic University/Smithsonian Institution.

PARATYPE 1, USNM E00042707 (Figures 3, 4C,E, 9C) AND PARATYPE 2, USNM E00042700 (Figures 7B, 9C). Calyx as in holotype, with interradial projections. Maximum calyx diameter 2.50 and 2.68 mm, minimum diameter 1.30 and 1.23 mm, height (including length of interradial projections) 1.55 and 1.88 mm, ratio of BB/RR height 0.56 and 0.62 (Figure 3A). Tegmen reaching middle or proximal margin of IIBr2 interradially. Tip of prominent anal sac level with base of Br4 terminating in relative high and broad terminal prominences (Figure 3C). Adoral triads of tube-feet each with high columnar base, especially developed in radii C and E (Figure 3C). Columnar bases of triads as well as soft tissue near mouth contain thin lacy plates.

Length of IBr1+2ax 2.37 and 2.38 mm; ratio IBr1/IBr2 height ~0.65 and 0.66. All free arms incomplete in paratype 1 and two arms complete in paratype 2; length of complete arms 29 mm with up to 44–45 IIBrs. Most frequent proximal free arm pattern 1+2 3+4 10+11 (6 of 11 cases). Most frequent position of P1 on IIBr7 (14 of 17 cases). P1 with 13–14 Pns, P 4 and 7 with 15 Pns each. Maximum number of successive muscular articulations 9. Rudimentary gonads occur at the bases of the proximal Ps. Every gonad is covered by Pn1 and is invisible externally (Figure 9C).

Both stalks complete, but broken into fragments. Total length of stalk from calyx to radix ~149.0 and 128.8 mm, total number of columnals 139 and 129. In paratype 1 diameter decreases from columnal 7 (1.30 mm) to 55 (0.84 mm), then increases slowly to 1.63 mm at columnal 138. In paratype 2 diameter decreases from columnal 7 (1.43 mm) to 36 (0.87 mm), then increases slowly to1.43 mm at columnal 128. Maximum ratio height/diameter of columnals 1.5 (in 85–90th columnals) and 1.68 (in 91th columnal); 54th and 57th columnals as hight as broad. Constriction at mid-height (never in proxistele) slightly or moderately developed in columnals 59 to136 and 50 to 125, and absent in the three distalmost. Mesistele synarthries as in holotype; distal synarthries circular with shallow ligament fossae. Fulcral ridge in all columnals as in holotype (Figure 4E). Long thin distal radicles attached to numerous grains of sand and foraminiferal tests (Figure 3B).

SPECIMEN FROM BAHAMAS, USNM 1021239 (Figures 7a, 8, 9A, B). Largest specimen with crown and stalk connected, ten arm fragments and two stalk fragments. Because this specimen differs significantly from the type specimens it is described in detail. Calyx conical, 2.20 mm high interradially; maximum and minimum diameters 4.12 and 2.30 mm; interbasal and interradial sutures conspicuous. BB/RR length ratio 0.69. Distolateral corners of RR not projecting interradially; adjacent primibrachs not separated. Surface of BB, RR and IBrs smooth and without longitudinal median convexity. Tegmen not compressed, high, rising interradially to Br4 or Br5. No visible ossicles on sides (in spaces between primibrachials). Top of prominent anal sac level with Br7, about 5 mm high. Ten short projections at top (Figure 8C).

Length of IBr1+2 3.87 mm; IBr1/IBr2 length ratio ~0.71; IBr1/R height ratio 1.4. IBrs broader distally than proximally, much broader than hight, their sides of slightly flattened into lateral flanges not continuing on to IIBrs. IBr2 without median prolongation.

All arms incomplete. Length of best preserved arm 50 mm having 55 Brs with 20 Ps on one side. Complete arm had about 95–100 Brs and 35 Ps on one side. Proximal pattern of free arms always 1+2 3+4 (10 cases), 3rd non-muscular articulation from Br8 to 14, 4th from Br13 to 21, 5th from Br17 to 27, 6th from Br24 to 35, variation range increasing from proximal to distal arm. Three arms with regeneration rudiments from Br7, 9 and 18. Maximum number of successive muscular articulations 9 before Br13 (2 cases) and 2 cases of 7 before Br11, number varying from 3 to 8 (mode 5) between Br10 and 30, decreasing beyond Br30 (mode 3). Longest arm fragment with distal end (53 Brs) never more than 4 successive muscular articulations (mode 3). Thorns lie along distal margin of Brs and Pns (Figures 8B, C).

P1 on Br7; in one case on Br6. On one side of an arm, every second or third Br bearing a P (Figure 8B). Minimum length of P1 11.2 mm with 16–20 Pns. Longest middle Ps of 31 Pns, up to 21 mm long. Most proximal and median Pns approximately equal in length; Pn3 usually not longer than Pn1. Pns crescentic in cross section with thorns externally along distal margin; distal Pns with lateral thorns. Each ambulacral groove bordered on both sides by rod-like spicules. Few sacculi were found only at the bases of proximal Ps. Small gonads are hidden under Pns1 (Figure 9A,B).

Stalk incomplete. Part attached to calyx composed of 124 columnals, 245 mm long. Two fragments of distal mesistele of 6 and 11 columnals; combined length 47 mm. Proximal columnals are quinquepartite. Stalk diameter increases from columnals 1 (2.20 mm) to 6 (2.35 mm); decreases between 7 and 32 to 1.85 mm (Figure 8F, D, E), remains the same (about 1.84–1.93 mm) from 32 to 60, and increases very slowly from 61 to 124 (2.51 mm). Columnal height increases from columnal 1 (0.25 mm) to 57 (2.51 mm), remains unchanged (~2.51–2.65 mm) between 57 and 115, and slightly increases to 2.80 mm by 124. Height/width ratio increases from columnal 6 (0.16) to 57 (1.3); columnal 41 is as long as broad. Sizes and proportions of columnals in the two fragments are the same as in columnals 121–124 of the stalk attached to the calyx. Mesistele synarthries like in other specimens.

This largest specimen differs from the other three small specimens (USNM E00042699, E00042707 and 1021239) in having more numerous Brs, Ps, Pns and columnals, a higher tegmen and shorter Pn3. These differences are most likely associated with age. However, some other differences may not be associated with age: interradial projections of calyx and large sacculi are present in the smaller specimens and lacking in the large one.

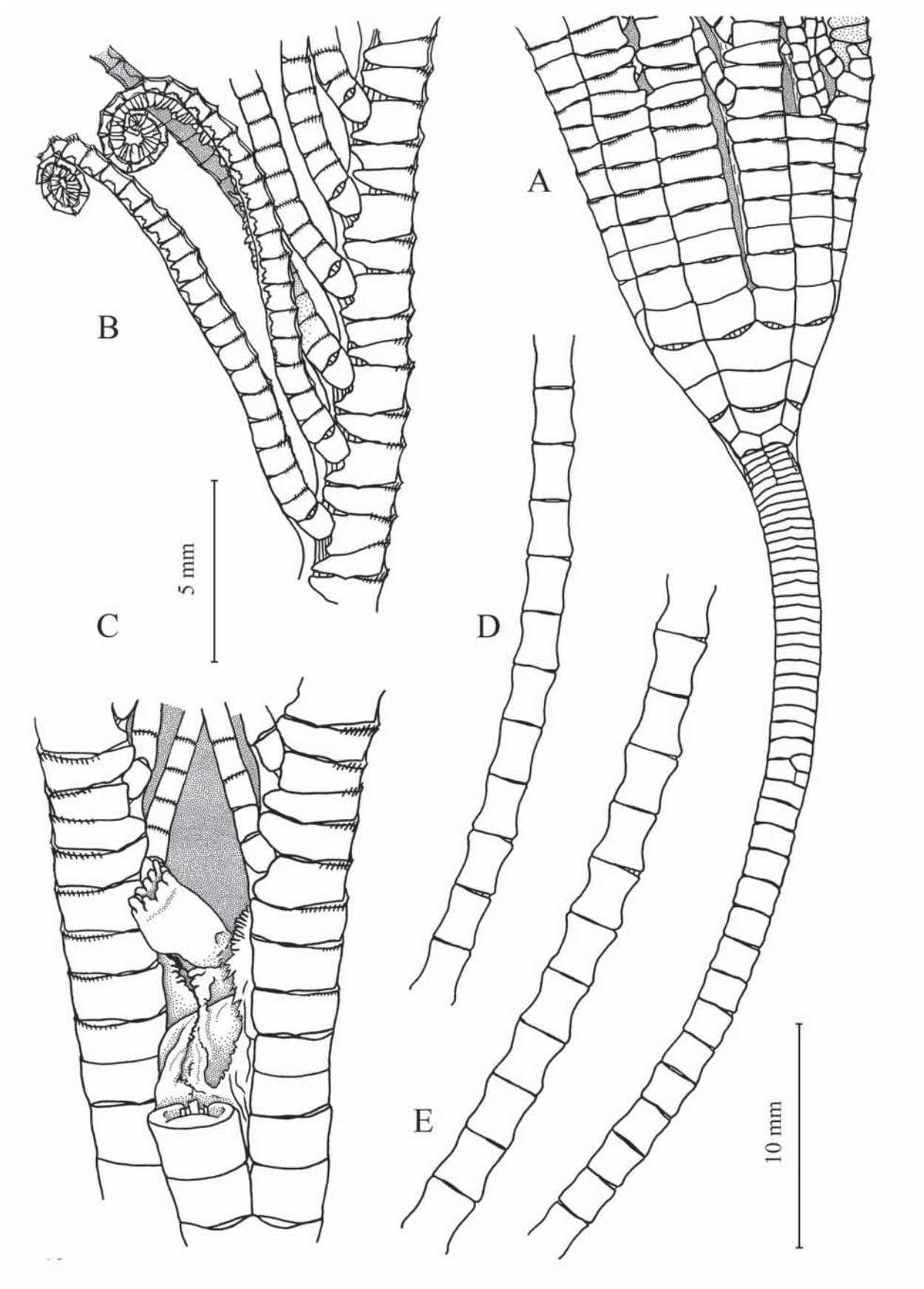SPECIMEN FROM FUERTE ISLAND, COLOMBIA, USNM E0017898 (Figure 9D).

FIGURE 8. *Rouxicrinus vestitus* new genus, new species, USNM 1021239. A. Calyx with proximal parts of stalk and arms. B. Pinnules 10 and 11 on the Br29 and Br31. C. Part of tegmen with anal sac. D. Stalk (median parts of mesistele) between 56th and 67th columnals. E. Stalk (distal parts of mesistele) between 107th and 118th columnals.
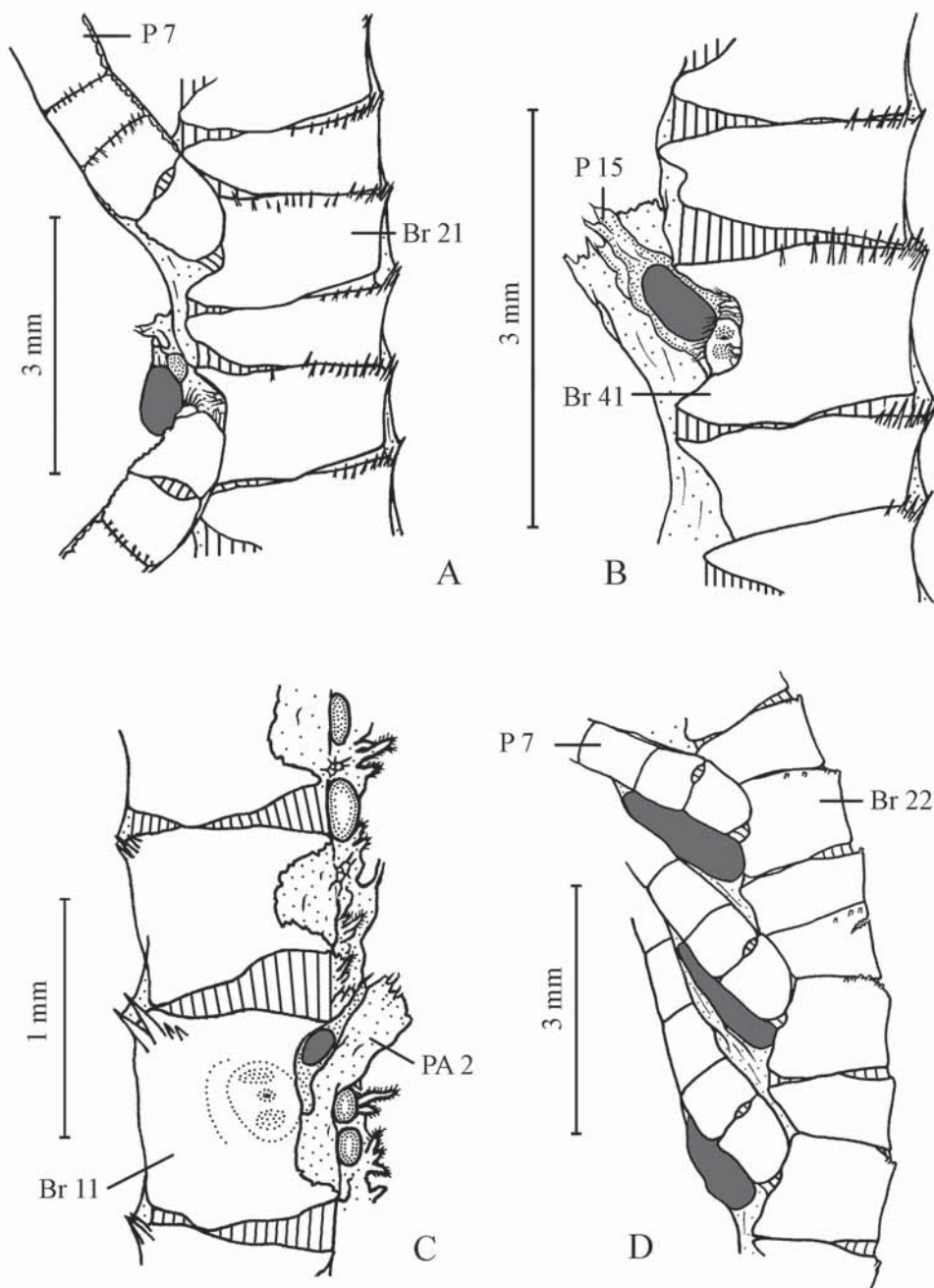
FIGURE 9. *Rouxicrinus vestitus* new species. Gonads in specimens of different size. A, B. Specimen USNM 1021239; P6 (together with gonad) are turned down (A), and P15 removed (B) to show the small gonads, which were not visible from exterior. C . Paratype USNM E00042707; PA2 from Br11 has been removed. D. Specimen USNM E0017898 with developed gonads readily visible from outside. Gonads are shaded.

The specimen in poor condition. Colour light yellowish-grey to whitish. Probably specimen has been fixed in formalin. Calyx with low interradial projections (relatively lower, than in the type specimens). Maximum and minimum calyx diameter 3.64 and 2.33 mm, height 2.24 mm, ratio of BB/RR height 0.65. Tegmen reaching proximal margin of Br5 interradially. Top of prominent anal sac level with Br9. Wide terminal opening of anal sac has side position and not bordered by projections.

Length of IBr1+2ax 3.81 mm; ratio IBr1/IBr2 height 0.90. One of arms lost, other are incomplete. Best preserved arm consists of 24 Brs. Most frequent proximal free arm pattern 1+2 3+4 7+8 (3 of 5 cases). Most frequent position of P1 on Br7 (3 of 5 cases). Pn3 longer than Pn1. Sacculi not observed because of poor condition of ambulacral grooves. Developed gonads are clearly distended (Figure 9D).

Stalk incomplete. Remaining proximal part of stalk (47 columnals) attached to aboral cup 42 mm long. A fragments of mesistele of 13 columnals. Some of proximal columnals compound. Tip of the stalk not tapering upwards. Stalk diameter decreases from columnals 1 (2.33 mm) to 23 (1.54 mm), and increases slowly from 24 to 47 (1.74 mm). Maximum stalk diameter in the mesistele fragment 1.83 mm. Columnal 38 is as long as broad; maximum height/width ratio 1.45 in the mesistele fragment.

This specimen differs significantly from the small (type) specimens in having whitish arms, a higher tegmen, different brachial patterns, large gonads, tip of stalk not tapering, and in lacking developed interradial projections of RR and terminal projections on the anal sac.

Distribution: Western tropical Atlantic, off Barbados, Fuerte Island (Colombia) and Bahamas, in depths of 421 to 887 m. This depth range is considerably shallower than previous records of species of Septocrinidae. *Septocrinus* is known from 5180–5190 m, *Zeuctocrinus* from 2000 to 6785 m.
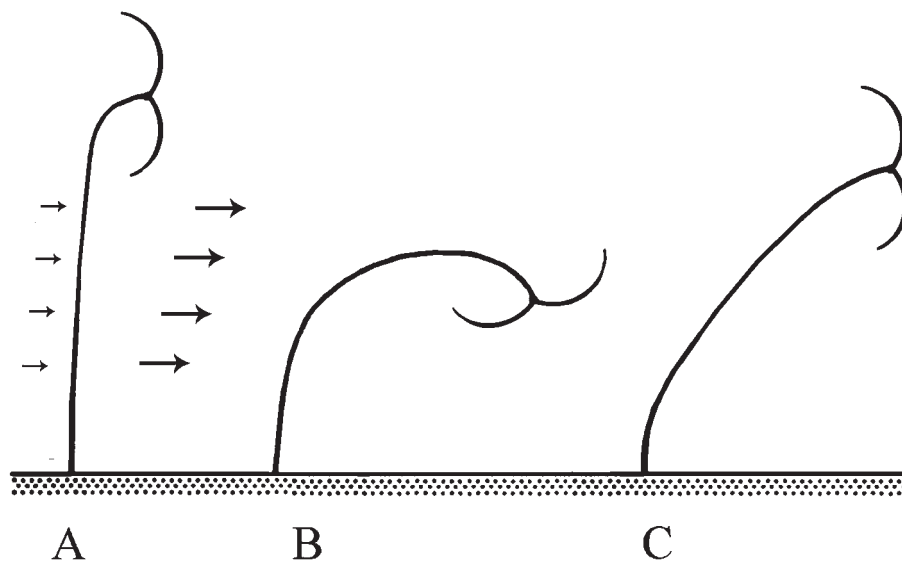

FIGURE 10. Feeding posture of the ten-armed stalked crinoids and their reaction to current flow. A. Feeding posture of *Rouxicrinus vestitus* in a gentle current; dististele with circular synarthries. B. Stalk posture of *Rouxicrinus vestitus* when current velocity increases rapidly (due to turbulence generated by the submersible). C. Feeding posture of ten-armed crinoid in a moderately high current; dististele with strongly elliptical synarthries. (C, after Roux, 1987, Fig. 3, 6C).

Notes on ecology and morphological adaptations

This species apparently prefers soft substrates. On Dive JSL-II-1737, the bottom was a 20° soft sediment slope with numerous burrows and mounds. On Dive JSL-II-1729, the bottom was flat, fine to coarse sand, with some burrows and conical mounds. On Dive JSLII-1734, the bottom was sandy, with many ripples. On Dive JSL-I-2268 off Bahamas the bottom was a steep slope with rock outcroppings and a veneer of smooth sand and mud. The bottom temperature was 7.5°C. *R. vestitus* was observed, photographed (Figures 7A, 7B), and videotaped off Barbados, at depths of 747–887 m: videotaped and photographed during JSL-I-1729 and JSL-II-1737, and photographed during JSL-I-2268 and JSL-II-1731. *R. vestitus* occurs widely scattered, not aggregated, on soft sediment, the stalk anchored by the root-like radix. Current velocity was usually about 8–10 cm/sec. All individuals deployed a filtration fan characteristic of many stalked crinoids: stalk more or less vertical; proxistele sharply bent so that the mouth orients downcurrent, and arms flexed back into the current. Juvenile specimens had ten complete arms, while the largest specimen, from Dive JSL-I-2268 (USNM 1021239), showed three broken, slightly regenerated, arms. Regenerating arms are frequently seen in stalked crinoids; injuries have usually been attributed to fish predation (Conan *et al.*, 1981; Roux, 1987). The stalks lacked obvious fouling.

D. Billett (videotapes of Dive 1737) observed the holotype of *Rouxicrinus vestitus* when the velocity and direction of current varied quickly (due to turbulence generated by the submersible). The crinoid passively

changed its posture in about 2 sec from mostly vertical to a sharply inclined stalk. At the inclined posture only the mesistele varied its form from slightly to sharply curved, whereas the sharply curved proxistele, almost straight dististele, and parabolic crown, retained their previous form (Figure 10). Once the stalk together with fan were swept (rotated) by turbulence about 45 degrees around the vertical axis. When the turbulence stopped, the mesistele rapidly returned to its previous straight posture. The mesistele of *Rouxicrinus vestitus* is evidently much more sensitive to rapid current changes than the dististele and proxistele. In this context the mesistele can be characterized as the most flexible part of the stalk. Morphofunctional analysis corroborates the in situ observations. The elliptical synarthries of the mesistele permit a greater amplitude of movement in comparison with circular synarthries (didtisistele) and circular synostoses (proxistele) (Roux 1987; Améziane & Roux, 2005).

A sharp bend of the *Rouxicrinus* proxistele at almost a right angle suggests its high plasticity. Recent study of crinoids reveal that stalk motility is under the control of contractile collagenous tissues (Baumiller and Ausich, 1996; Baumiller, 2008; Birenheide and Motokawa, 1996; Grimmer *et al.*, 1984; Wilkie *et al.,* 1993). Collagenous tissues cannot contract actively, but their tensile properties can be varied rapidly. Additionally, the 'catch' (lock) properties allow an individual to hold a position for a long time. Proxistele plasticity depends positively on the number of small ossicles and collagenous/calcite ratio. These two dimensions increase significantly if the proxistele columnals are divided into separated pieces. Extreme fragmentation of proxistele columnals in *Vityazicrinus petrachenkoi* (Vityazicrinidae), *Dumetocrinus antarcticus* and *Feracrinus aculeatus* (Hyocrinidae) (Mironov, Sorokina, 1998, Figures 3.10, 4.5 and Plate 2.6) seems to be a stabile adaptation ensuring high plasticity of the proxistele.

Numerous examples of compound columnals can be found in the Paleozoic (Rozhnov, 2002, Figure 4; Stukalina, 1986, Figures 7–10, Plates 4–6; Ubaghs, 1978, Figures 45, 48, 60, 63; and others). Paleozoic evolution of the stalk was directed from the quinquepartite columnals with pentameres placed at different levels to pentameres arranged in horizontal rows divided by five longitudinal sutures; then followed progressive disappearance of the quinquepartite columnals and introduction of monolithic columnals (Sieverts-Doreck, 1957, Stukalina, 1967, 1986; Ubaghs, 1978). However, the stalks of the Paleozoic crinoids with pentameres placed at same level are very small compared with the multipartite proxisteles of the extant crinoids which are composed of numerous irregularly arranged skeletal pieces. It may be noted also that some extant stalked crinoids usually with monolithic proximal columnals show occasional fragmentation as a consequence of anomalous stalk growth. For example, a few compound proximal columnals have been observed in *Anachalypsicrinus nefertiti, Guillecrinus reunionensis* and *Porphyrocrinus verrucosus* (Mironov and Sorokina, 1998, Figure 8.3; Améziane and Roux, 2005, Figure 1g, h; Messing, 2007, Figure 4a).

In *Rouxicrinus vestitus* the limited mobility of each synostosis is compensated for by the large number of discoidal columnals and attachment of the tapering proxistele to the calyx, mainly by collagenous tissue (Figure 1A). Other species of Septocrinidae have very short proxisteles with a few discoidal columnals. In *Septocrinus disjunctus* the short proxistele is compensated for by division of two most proximal columnals into pieces, widely separated from each other by collagenous tissue .

Comparison of the morphology of *R. vestitus* and Bathycrinidae indicates that the arms in the former are more flexible (with more numerous muscular joints), the fan is more dense, the mesistele more flexible (shorter columnals) and the dististele less flexible (less ovoid elongation of the articular facets) (compare the figures 10B and 10C).

The development of interradial projections of RR in *Rouxicrinus vestitus* and *Septocrinus disjunctus* provides reinforcement of the arm bases. In the Bathycrinidae a similar function is performed by the inner knobby processes on adjacent primibrachials which come into contact with each other. With increase of body size RR and IBr1 become usually less elongated and the articular area between them becomes relatively larger. For this reason the need to reinforce the arm bases decreases as body size increases. The lack of interradial projections on the RR of the larger specimens of *Rouxicrinus vestitus* may just be a consequence of the shorter/wider proportions of its RR and IBr1relative to the apparently more elongated proportions in the smaller specimens.

The sacculi are numerous in the smaller specimens of *Rouxicrinus vestitus*, but few in the largest specimen. Sacculi are common in the Comatulida; the superfamily Comasteracea is the only extant comatulid superfamily in which sacculi are not regularly found. They are absent in all of Comasteridae except for *Comatilia iridometriformis* (Messing, 1984). Carpenter (1884, p. 127) noted, that "though structures of the same nature occur sparingly in *Pentacrinus*, *Rhizocrinus*, and *Bathycrinus*, they are but poorly developed and irregular in their occurrence". Sacculi are absent in *Holopus*, but "sacculus-like structures" were observed in *Gymnocrinus* (Heizeller *et al.*, 1994). We found sacculus-like structures in *Monachocrinus recuperatus* and *M. aooteanus* and did not find sacculi in other Bathycrinidae, nor in Hyocrinidae, *Guillecrinus*, *Vityazicrinus* and *Conocrinus lofotensis*.

The function of the sacculi is obscure. They were regarded as mucous glands by Bury (cite on Carpenter, 1884 and A.H. Clark, 1921). A.H. Clark (1921) listed eleven hypotheses about sacculi function, favoring their function as excretory organs. Hyman (1955, p. 50) wrote: "possibly they represent protein reserves, although they have not been observed to be utilized in starvation or regeneration." Holland (1967) interpreted sacculi as light-sensitive lenses. The latter interpretation is not applicable to the septocrinids inhabiting aphotic zones. It is noteworthy that ambulacral grooves in the Septocrinidae (as well as in the most Comatulida with sacculi) are not bordered by cover plates. They are poorly canalized and perhaps not very efficient at transporting food particles to the mouth. This seeming deficiency can be compensated for in one of two ways: (1) by local utilization of food near the ambulacral grooves, or (2) by producing a great amount of mucus. In light of these possibilities, we suggest two alternative functions for sacculi: (1) local digestion or (2) mucus production.

The gonads are usually well developed in the larger specimens of Bathycrinidae and Hyocrinidae. Duco and Roux (1981) characterized *Bathycrinus carpenteri* as having "continuous gametogenesis" (multiple spawning). The gonads occur in the proximal pinnules of Bathycrinidae and Hyocrinidae. The location within the V-shaped pinnules would make them relatively inaccessible to predation by fishes. Gonads were not reported for *Septocrinus disjunctus* and *Zeuctocrinus spiculifer*, they are small in *Zeuctocrinus gisleni* (A.M. Clark, 1973) and *Rouxicrinus vestitus,* except for the specimen E0017898 (Figure 9). The lack of the conspicuous gonads in most septocrinids examined probably indicates that they (in common with many comatulids) pass through a long unsexable phase during the reproductive cycle. The septocrinid pinnules lack protected (covered) spaces for gonads. For this reason, protection of the gonads under conditions of great predator pressure is achieved by other ways: presence of a long unsexable phase and location of the gonads under Pn1.

Acknowledgements

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